

Salt Tolerance Research in Date Palm Tree (*Phoenix dactylifera* L.), Past, Present and Future Perspectives

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1 **Salt Tolerance Research in Date Palm Tree (*Phoenix dactylifera* L.), Past, Present and**
2 **Future Perspectives**

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23 **Abstract**

24 The date palm can adapt to extreme drought, to heat, and to relatively high levels of soil
25 salinity. However, excessive amounts of salt due to irrigation with brackish water lead to a
26 significant reduction in the productivity of the fruits as well as marked decrease in the viable
27 numbers of the date palm trees. It is imperative that the nature of the existing salt-adaptation
28 mechanism be understood in order to develop future date palm varieties that can tolerate
29 excessive soil salinity. In this perspective article, several research strategies, obstacles, and
30 precautions are discussed in light of recent advancements accomplished in this field and the
31 properties of this species. In addition to a physiological characterization, we propose the use
32 of a full range of OMICS technologies, coupled with reverse genetics approaches, aimed
33 towards understanding the salt-adaption mechanism in the date palm. Information generated
34 by these analyses should highlight transcriptional and posttranscriptional modifications
35 controlling the salt-adaptation mechanisms. As an extremophile with a natural tolerance for a
36 wide range of abiotic stresses, the date palm may represent a treasure trove of novel genetic
37 resources for salinity tolerance.

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44 **Key words:** salinity, date palm, omics, abiotic stress, reverse genetics, *Phoenix dactylifera* L.

45 **Running title:** Salinity tolerance in *Phoenix dactylifera* L.

46 **Impact of soil salinity on date palm**

47 It is widely believed that the date palm originated in the ancient Mesopotamia region or in
48 western India (Wrigley, 1995). Currently, the date palm is the primary crop in several arid
49 and semiarid countries in North Africa, the Middle East and Central America (Food and
50 Agriculture organization of the United Nations, 2006). For example, in Oman, the date palm
51 occupies about 50% of the cultivated area and comprises 82% of all fruit crops grown in the
52 country.

53 Salinity is the leading problem affecting agricultural production and ecosystems around the
54 world. In recent decades, excessive soil salinity has become a global agricultural constraint
55 (Rengasamy, 2006; Munns and Tester, 2008). This holds especially true in arid and semiarid
56 regions where a considerable amount of agricultural land area has been affected (Pitman and
57 Läuchli, 2002) and has led to significant economic losses in date palms and other crops
58 (Cookson and Lepiece, 2001). This problem is more prevalent and the implications of the
59 losses are more compelling in Oman and other Persian Gulf states due to the high evaporation
60 rates from the soil surface (Stanger, 1985). The major causes of increased soil salinity in arid
61 and semiarid regions are insufficient rainfall coupled with over-irrigation using brackish or
62 saline groundwater (Hillel, 2000; Pitman and Läuchli, 2002; Malash et al., 2008). Soil
63 salinity has resulted in desertification of large agricultural areas, particularly in coastal areas
64 where the overharvesting of water has led to an infiltration of seawater into the groundwater
65 (Stanger, 1985).

66 **Salt-adaptation capacity of the date palm**

67 The date palm tree has evolved through natural selection to be a drought- and salt-tolerant
68 plant (Zaid and De Wet, 2002a) with an adaptation capacity exceeding barley, which is
69 widely considered to be a salt-tolerant crop (Furr and 1975). Some date palm varieties have

70 the ability to grow in close proximity to the seashore where they are often exposed to
71 seawater during tidal currents. Therefore, the date palm could be considered one of the
72 exceptional halophytic plants and may possess a suite of mechanisms for salinity tolerance.

73 Plant species vary in their responses to saline conditions. While salt-tolerant plants have the
74 ability to cope with a relatively high level of soil salinity, susceptible plants are not able to
75 grow under the same salinity conditions (Munns and Tester, 2008). Soil salinity causes ionic
76 toxicity and osmotic stress in salt-susceptible plants, a situation that reduces the growth rate
77 and may lead to plant death. Very little scientific information is available regarding salt
78 tolerance in the date palm. Ramoliya and Pandey (2003) screened particular date palm
79 varieties for their salinity adaptive capacity and found that certain varieties can endure a
80 relatively high soil salinity level of $12.8 \text{ dS}\cdot\text{m}^{-1}$ ($1 \text{ dS}\cdot\text{m}^{-1} = 640 \text{ mg}\cdot\text{l}^{-1}$) with no visible effect
81 on the seedling phenotype. Another study conducted by Alrasbi and colleagues (2010) found
82 that some other date palm varieties can tolerate up to $9 \text{ dS}\cdot\text{m}^{-1}$ soil salinity, and an excess of
83 Na^+ ions accumulated in the leaves of the plants treated with high salt concentrations.
84 Nevertheless, much work at the physiological and molecular levels is required in order to
85 fully understand the salt-adaptation mechanisms in the date palm.

86 **What is known about salinity adaptation mechanisms in the date palm?**

87 Plants can adapt to soil salinity through three major mechanisms: i) osmotic tolerance, ii) Na^+
88 or Cl^- exclusion and secretion, and iii) accumulation of Na^+ or Cl^- in the tissues (Munns and
89 Tester, 2008). These strategies involve different mechanisms, including the production of
90 compatible solutes (Munns and Tester, 2008) such as sugars and sugar alcohols (e.g.,
91 trehalose, mannitol, and galactinol); the synthesis of amino acids and amines (e.g., proline
92 and glycine betaine); the induction of free radical scavengers, such as superoxide dismutase
93 (Hazman et al., 2015); the modulation of genes encoding transporters responsible for ionic
94 balance, such as Na^+/H^+ antiporters and other Na^+ transporters (Reguera et al., 2013), Na^+

95 uniporters and/or ion channel-type transporters (Craig Plett and Moller, 2010; Assaha et al.,
96 2015); the accumulation of late embryogenesis abundant (LEA) proteins (e.g., dehydrins)
97 (Hanin et al., 2011; Jyothi-Prakash et al., 2014); and the alteration of the hormonal contents
98 of leaves and roots, such as abscisic acid (ABA) (Mittler and Blumwald, 2015), indole acetic
99 acid (IAA), and ethylene (Yaish et al., 2015). Additionally, plants trigger their epigenetic
100 machinery to activate or deactivate various genes involved in salt tolerance, including
101 miRNA biogenesis (Chaabane et al., 2012; Macovei and Tuteja, 2012) and DNA methylation
102 processes (Tan, 2010; Jiang et al., 2014).

103 Despite the fact that molecular pathways underlying salt-adaptation mechanisms in some
104 plant species have been dissected and partially identified, these mechanisms in the date palm
105 still remain unknown. Previous work on salt-adaptation of date palm trees has focused on the
106 genetic differentiation of adaptive varieties using DNA marker analysis, such as random
107 amplified polymorphic DNA (RAPD) (Sedra et al., 1998; Kurup et al., 2009) and
108 microsatellites (Elshibli and Korpelainen, 2008). However, these analyses did not localize
109 functional genes linked to salt-adaptation traits in this plant.

110 Additionally, work using date palm cell suspension cultures to investigate the response of
111 palm cells to salinity has been recently reported (Al-Bahrany and Al-Khayri, 2012). The
112 growth of these cells was negatively affected by salt treatment and the cellular Na⁺ content
113 initially increased and then decreased within a few days of the treatment (Al-Bahrany and Al-
114 Khayri, 2012). Furthermore, the proline levels were directly correlated with the NaCl
115 concentration in the callus (Al-Khayri, 2002) and in the early-stage seedlings (Djibril et al.,
116 2005). This type of study that is performed on cells or tissues generated *in vitro* can provide
117 some information about the nature of salt-adaptation mechanisms. However, data from
118 undifferentiated plant tissues lack the important functional input of various differentiated and
119 well-developed tissues in the adaptation mechanism.

120 Recently, the date palm genome (*Khalas* variety) was sequenced (Al-Dous et al., 2011; Al-
121 Mssallem et al., 2013), a genetic map was constructed (Mathew et al., 2014), and a group of
122 conserved miRNA was computationally characterized (Xiao et al., 2013) based on the
123 genome of the same variety. Moreover, gene expression analysis was performed on different
124 plant tissues (Bourgis et al., 2011; Zhang et al., 2012); however, there is no gene expression
125 or genetic marker data associated with salinity tolerance or any abiotic stress in date palms. In
126 comparison with a few other date palm varieties, *Khalas* exhibited a higher level of salinity
127 tolerance (Aljuburi, 1992; Al-Mulla et al., 2013). Therefore, it might be used as a standard
128 variety by the research community given that the information generated by OMICS analysis,
129 using this variety, has some advantages in salinity tolerance research. However, it is difficult
130 to know if *Khalas* is the most tolerant among the other varieties because a comprehensive
131 study screening a large number of date palm varieties for their salinity tolerance is still
132 unavailable.

133 **How can the salinity-adaptation mechanism in the date palm be deciphered?**

134 Although date palms have the ability to grow under saline conditions, different varieties have
135 displayed distinct levels of tolerance to soil salinity. Indigenous varieties growing in
136 relatively saline soils and showing a normal phenotype may possess genes responsible for a
137 more efficient salinity adaptation mechanism than those growing in less saline soils. However,
138 the question remains as to how these plants are able to grow in such a condition while others
139 cannot. Do they exclude, compartmentalize, or secrete the NaCl? Do their tissues possess
140 unique osmotic tolerance mechanisms? In order to find answers for these questions, varieties
141 of date palms growing around the world should be characterized. A starting point would be to
142 perform essential physiological and morphological characterizations (including growth rates,
143 histology, tissue content, ion transport, etc.) (Yeo et al., 1999; Gong et al., 2006; Faiyue et al.,
144 2012). From these, a small group of extremely salt-tolerant and salt-susceptible varieties

145 should be studied in depth. It is known that some other salt-tolerant species, such as
146 mangroves, develop specific apoplastic barriers that can act as filters against NaCl uptake in
147 their roots, minimizing the salt movement into the plant (Krishnamurthy et al., 2011;
148 Krishnamurthy et al., 2014a). Hence, we should also study the kinetics and dynamics of salt
149 uptake or salt exclusion in roots as well as the histology of the roots in both tolerant and
150 susceptible date palm varieties.

151 With trends leading to a greater production of date palm trees with enhanced salinity adaptive
152 traits, the knowledge generated by Next Generation OMICS technologies should lead to a
153 better understanding of the salt-adaptation mechanisms in the date palm. Thus, comparative
154 RNAseq, differential proteomics and metabolomics, and the use of biochemical tools to
155 understand the metabolic pathways associated with enhanced tolerance may lead to the
156 discovery of novel gene(s) and metabolic pathways associated with salt-adaptation in date
157 palms. Heterologous expression analysis in model plants could be used for the subsequent
158 functional characterization of candidate genes. The generation of knockout mutants in the
159 date palm would allow the application of reverse genetics to identify and characterize the
160 function of unknown genes in the long term.

161 Several genome and transcriptome projects have been accomplished in the past to identify
162 key genes for salt tolerance in various plant species. Unfortunately, the outcomes of these
163 projects were rather modest because adaptation to salt is a multigenic trait in plants (Wang et
164 al., 2012; Leonforte et al., 2013). A recent proteomic analysis of membrane proteins from the
165 mangrove tree *Avicennia officinalis* helped to identify numerous membrane transporters and
166 other membrane-integral proteins (Krishnamurthy et al., 2014b). However, on its own, this
167 study was unable to provide a mechanistic basis for the salt tolerance exhibited by the
168 mangroves, and it can only serve as a basis for future investigations into the mechanism.

169 Reverse genetics, which is based on loss- and gain-of-gene function principles, is a powerful
170 method in functional genomics research (Colbert et al., 2001). This tool can also be used to
171 study salinity tolerance in the date palm. Various strategies to generate random point
172 mutations, such as ethyl methane sulfonate (EMS) and ionizing radiation treatments and the
173 use of RNAi, transposon and T-DNA mutagenesis approaches, help identify genes associated
174 with salinity tolerance based on the phenotype of the screened mutants. This technology,
175 coupled with the next generation sequencing (NGS) tools, will allow multiplexing of gene
176 targets thereby providing a greater chance of locating the target genes. However, these
177 strategies require the establishment of an efficient propagation and *Agrobacterium*-mediated
178 genetic transformation protocols for the date palm (Mousavi et al., 2014).

179 Taken together, this suggests that deciphering salt-adaptation mechanisms based on the
180 variation in a single cellular product category (i.e., transcript or protein abundance in
181 isolation) between salt-treated and untreated seedlings is unlikely to generate enough
182 information that provides a more complete picture. However, the use of multi-disciplinary
183 techniques (and multi-OMICS tools) to analyse various cellular products may provide a
184 higher possibility of detecting additional elements associated with this phenotype in the date
185 palm. Such an approach will undoubtedly make the genetic manipulation process, which aims
186 to further improve salt-adaptation, more objective and efficient. For example, the information
187 obtained from digital gene expression (DGE) analysis alone may not lead to the identification
188 of key genes and mechanisms associated with salinity adaptation capacity in the date palm.
189 However, combining that study with a global proteomics and hormonal analysis may lead to
190 the discovery of critical pieces of the puzzle in this mechanism. It is worth highlighting in
191 this context that studying the posttranslational modifications of membrane transporter
192 proteins is a priority since these proteins may not vary in their amounts, but their levels of
193 posttranslational modifications, such as phosphorylation in response to saline conditions, may

194 vary significantly. Being a complex trait at both the genetic and physiological levels, such
195 experiments may deliver important information that can be adopted by plant breeders to
196 improve salinity tolerance in the date palm. Again, this may be achieved by transgenic means
197 or by generating genetic crosses when the genes are present in closely related species or
198 varieties. Consequently, the discovery of salt tolerant gene(s) will help breeders to select
199 parent varieties (germplasm) and progenies using the marker-assisted selection strategy.

200 The outcome of the physiological and multi-OMICS analyses may provide answers to the
201 following fundamental questions:

- 202 1) What is the most salt-adaptive date palm variety?
- 203 2) What is (are) the mechanism(s) behind salt-adaptation in the date palm tree?
- 204 3) Which genes are responsible for the salt-adaptation in roots and leaves?
- 205 4) Is there a crosstalk between the genetic network in roots and leaves during the
206 adaptation procedure?
- 207 5) What are their gene products and their effects on the phenotype?
- 208 6) What are the posttranslational modifications associated with salinity tolerance in
209 the date palm?

210 **Obstacles facing salt tolerance research in the date palm**

211 There are hundreds of different varieties of date palm with distinct names; however, only a
212 few of these are dominant and are being actively cultivated (Krueger, 1998). The
213 nomenclature as well as the genetic makeup of date palm varieties varies from one country to
214 another. This is a confusing situation that leads to complications. Therefore, worldwide
215 nomenclature standardization is a necessity for successful date palm research. This should be
216 accompanied by the establishment of an international germplasm bank through which defined
217 germplasm can be accessible. This will facilitate seed exchange between laboratories and will
218 enable various research lines in date palm, including salt tolerance research.

219 Date palms have a long juvenile period with the minimum generation time (from seed to
220 seed) ranging from five to seven years. Therefore, any classical genetic breeding or
221 quantitative genetic program (Fan et al., 2015) aiming to decipher and enhance salinity
222 tolerance is a time- consuming process. However, the use of modern biotechnological tools in
223 this respect involving direct genetic manipulation, such as genetic engineering, may offer
224 suitable solutions. Experiments aimed at salinity tolerance require the use of plants with well-
225 defined genetic backgrounds. Such plants will have relatively uniform developmental stages,
226 which will help to obtain reliable results. Therefore, we maintain that the use of genetically
227 divergent adult trees or asexually reproduced basal offshoots growing in the field (whose
228 growth is not under controlled conditions) and used to carry out differential experiments is
229 unsatisfactory.

230 Date palm is a perennial dioecious fruit plant. Fruits are normally produced by cross-
231 pollination with pollen grains acquired from male flowers of different date palm sources
232 (Zaid and De Wet, 2002b). Farmers often select pollen grains for the pollination process
233 based on the availability and the compatibility of the pollen grains with various varieties
234 during a certain time of the season. Therefore, screening for salt tolerance using seeds of
235 different varieties is also not technically acceptable because of the possible difference in
236 paternal genetic background of the same variety. Under controlled conditions, this problem
237 can be resolved by using a uniform paternal genetic background. In this strategy, flowers of
238 different varieties can be pollinated using a common source of pollen grains. However, this
239 approach does have some limitations; for example, female and male varieties may flower at
240 different times or may not be compatible.

241 Another source of genetically homogenous varieties could be tissue culture-derived date palm
242 plantlets (Zaid and De Wet, 2002). However, this strategy has its own limitations. One such
243 constraint is the availability of a wide range of date palm varieties in the commercial tissue

244 culture laboratories. Other restrictions include the presence of somatic variations between
245 plantlets of the same variety and the possible malformation of root systems due to the use of
246 excessive amounts of hormones during the tissue culture process. These abnormalities may
247 affect the subsequent physiological and molecular results.

248 In conclusion, despite being one of the oldest cultivated trees (Nixon, 1951; Zohary and
249 Hopf, 2000), only a relatively small amount of research has been done regarding salinity
250 adaptation mechanisms in the date palm. Research aimed at achieving a better understanding
251 of this mechanism represents a golden opportunity for scientists to decode a black box of
252 genetic resources that have evolved and developed in severe abiotic stress conditions for a
253 super-tolerant phenotype. Since conventional breeding of the date palm is an arduous
254 procedure, scientists should take advantage of the recent advances in Next Generation
255 OMICS technologies. Complementary research should focus on the physiological changes
256 associated with salinity tolerance. Together, information obtained from these research lines
257 may provide a comprehensive view of salinity tolerance in date palms and facilitate the
258 development of applications towards improving the salinity tolerance of this important crop.

259

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